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Taxonomy and historical biogeography of the genus *Rhyacophila* Pictet, 1834 on the Philippines

(Insecta, Trichoptera)

With 30 figures and 3 tables

Wolfram Mey

Zusammenfassung

Die Gattung *Rhyacophila* ist auf den Philippinen mit 9 Arten vertreten. Davon werden hier fünf neue Arten beschrieben: *R. baldensis* sp. n., *R. banahawmontis* sp. n., *R. amoyanensis* sp. n., *R. pilifera* sp. n., und *R. cordilliera* sp. n. Die Genitalapparate der Männchen und die Imagines von vier Arten werden abgebildet. Die Arten verteilen sich auf die *castanea*-Gruppe und die neu aufgestellte *spinosellata*-Gruppe. Zwei Punktkarten zeigen die Verbreitung der Gruppen auf den Philippinen. Die Verwandtschaftsverhältnisse werden in drei Kladogrammen dargestellt, die auf der Analyse genitalmorphologischer Merkmale beruhen. Die Arten der *castanea*-Gruppe sind über Borneo auf die Philippinen eingewandert. Die *spinosellata*-Gruppe ist endemisch auf den Philippinen. Ihre Arten werden als Reliktendemiten angesehen, da die nächsten Verwandten in Ostasien und Japan vorkommen, und die Artengruppe ansonsten in ganz Südostasien fehlt. Die möglichen Ausbreitungsmechanismen werden kurz diskutiert.

Summary

Nine species of the genus *Rhyacophila* occur on the Philippines. Five species are described as new: *R. baldensis* sp. n., *R. banahawmontis* sp. n., *R. amoyanensis* sp. n., *R. pilifera* sp. n., and *R. cordilliera* sp. n. The male genitalia and adults of four species are illustrated. The species belong to two species-groups, with the latter group established herein. The ranges of these groups in the Philippines are depicted in two maps. Phylogenetic relationships were analysed and are presented in three cladograms based on morphological characters of male genitalia. The species of the *castanea*-group immigrated into the Philippines via Borneo, whereas the species of the *spinosellata*-group are relict elements of an older Asian fauna. A dispersal scenario is proposed for both groups concerning the colonisation of the Philippines.

Key words

Insecta, Trichoptera, *Rhyacophila* Pictet, new species, taxonomy, phylogeny, historical biogeography, dispersal scenario, Borneo, the Philippines

1. Introduction

The Rhyacophilidae and its large genus *Rhyacophila* Pictet, 1834 represent one of the most ancestral branches within Trichoptera. The group has retained many primitive characters especially in wing venation and genital architecture. According to the fossil record the genus is at least Eocene in age, and probably much older (Ulmer 1912, Mey 1988, Wichard et al. 2009). Since most of the Philippine Islands originated only in the Miocene (Hall 1996) the existence of the genus

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predates the formation of this archipelago. The presently known *Rhyacophila* species on the islands are the result of colonisation processes which started as soon as the islands appeared from the sea. The colonisation history, however, seems to be very complex. It is closely connected with the complicated and puzzling development of maritime South East Asia, including Taiwan, Sundaland and Sulawesi. The Trichoptera fauna of the past was surely as dynamic as it is today. The present-day pattern of its composition and distribution in the area is the result of dispersal, vicariance and subsequent evolution, with dispersal as the principal process in an oceanic environment (Cowie & Holland 2006). These processes are more or less imprinted in the distribution pattern in the archipelago, and their analyses could possibly enable the reconstruction of their colonisation history. The genus *Rhyacophila* appears to be a promising candidate for undertaking such an analysis. The quality of the study depends on the available data. A comprehensive inventory and an advanced level of faunistic research could provide the necessary facts. Both information sources are, however, weakly developed in the Philippines. Present knowledge is inadaquate, and we know only parts of the fauna, which are but large enough to recognise the presence of a diverse fauna with a high percentage of endemism. This poor faunistic and taxonomic basis prompted the author to perform a series of field trips to the Philippines from 1994 to 2001. Samples of caddisflies were taken on all major islands. This material forms the principal basis of the present study.

In the 1990s the environmental devastation of large stretches of rainforests and rivers on the Philippines was already at an advanced stage. Many visited areas were devoid of suitable habitats for stenoecious caddisflies and already possessed an impoverished fauna. An unknown number of *Rhyacophila* populations and probably even endemic species must surely have gone extinct. By now it is no longer possible to achieve a substantial survey of the original distribution of species and communities. The fauna is much reduced and consequently the collected data, although considerable, cannot be significantly increased. Any faunistic or biogeographic research in the Philippines today is actually the study of a fragment out of a fragment. Devastation processes go on in all parts of the country (Broad & Cavanagh 1993, Heaney & Regalado 1998). Nearly 20 years ago Wilson (1992) wrote: "Today the Philippine fauna stands on the eve of comprehensive destruction caused by deforestation and the poverty of an increasing human population." The eve is over. The loss of Philippine diversity is now a reality. Nevertheless, the study of the fauna remains an urgent task, at least to recover the information that still can be saved.

2. Material and methods

Collecting:

Adult caddisflies were collected using light. Usually, a light-tower (with 2 superactinic tubes, 12 W) was placed in the vicinity of rivers, and the arriving caddisflies were picked up from the gauze sheet that surrounds the tubes. Collecting usually started at sunset and was finished after 3-4 hours. The collected specimens were partly put in 75 % alcohol and partially pinned the next day. During daytime, specimens were captured using a hand-net in the bank vegetation.

Genital preparations:

The abdomen was boiled in KOH for some minutes to macerate the muscles, body fat and internal, unsclerotised structures. The abdomens were stained with Chlorazol Black after which the preparation was washed in 70 % ethanol. At this point the abdomen was studied in detail. It was turned in all directions in order to understand the shape and position of its individual components, and all the relevant abdominal and genital structures were now drawn in dorsal, ventral,

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lateral and/or caudal view. A drawing tube attachment to the binocular microscope (Leica, Wild M8) was used. After study the genitalia were deposited in polyethylene genitalia vials (BioQuip Products) filled with glycerin. The vials were attached to the pin.

Deposition:

Most of the material was preliminarily stored in the Museum für Naturkunde Berlin. Individuals of all species, including paratypes, are to be deposited later in a museum in the Philippines.

Abbreviation of depositories:

MFN	Museum für Naturkunde, Berlin
USNM	National Museum of Natural History, Smithsonian Institution, Washington

3. Results

3. 1. Taxonomy

Check-list of *Rhyacophila* species from the Philippines

R. castanea-group

R. davao Ross, 1950	Mindanao
R. negrosana Mey, 1998	Negros
R. banahawmontis sp. n.	southern Luzon
R. baldensis sp. n.	northern Luzon

R. spinosellata-group

R. cataractae Mey, 1998	Negros
R. spinosellata Mey, 1994	Mindoro
R. tenebrosa Mey, 1998	Mindanao
R. amoyanensis sp. n.	Palawan
R. pilifera sp. n.	southern Luzon
R. cordilliera sp. n.	northern Luzon

Description of new species

***R. castanea* - group**

***Rhyacophila baldensis* sp. nov.**

(Figs 1-3, 21)

Holotypus ♂, Philippines, Luzon, Mountain Province, village Chatol, 2100 m, 17°02 N 121°03 E, 16. - 18.11.1997, leg. W. Mey & K. Ebert (MFN).

Paratypes: 2 ♂♂, Luzon, Nueva Viscaya, Santa Fé, Bald Mountains, 1150 m, 11. – 13.11.1997, leg. W. Mey & K. Ebert (MFN); 2 ♂♂, Luzon, Mountain Province, Barlig, 17°03 N 121°04 E 1650 m, 14. – 15.11.1997, leg. W. Mey & K. Ebert (MFN); 1 ♂, Luzon, Ifugao, Mount Polis, 2000 m, 17°01.55 N 121°02.48 E, 13.11.1997, leg. W. Mey & K. Ebert (MFN).

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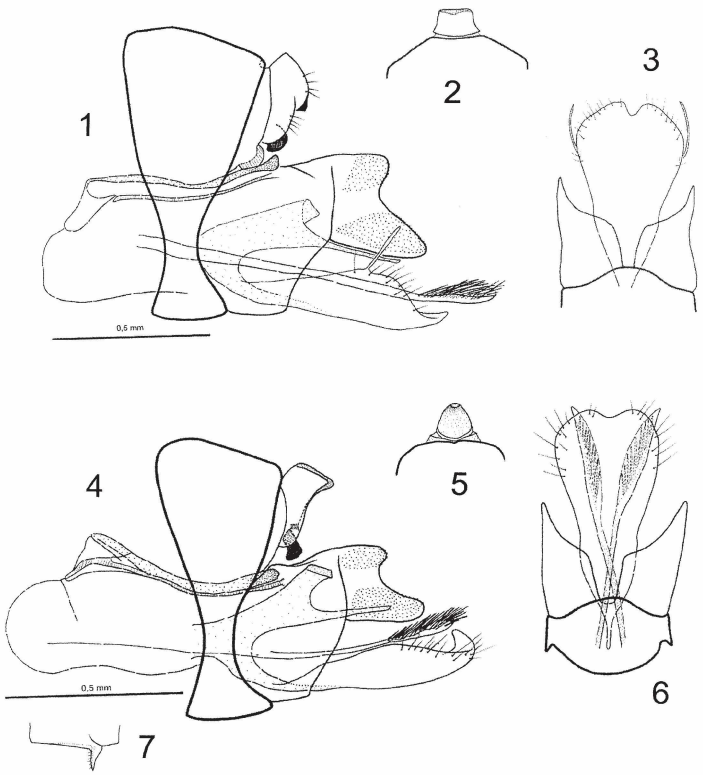
Derivatio nominis:

The species is named after the Bald Mountains, south of the Central Cordilliera, where *R. baldensis* sp. n. was collected the first time.

Length of forewing 6 – 6.5 mm, wing-span 13 – 14 mm; head and thorax dark brown; antenna brown, the basal third yellow-brown; ocelli white; forewings dark brown with numerous small white spots scattered over the whole forewing; basal parts of veins with erected, black bristles; fork 4 in forewing as long or longer than its stalk; hindwings pale brown; abdomen black dorsally; abdominal segment VII with short sternal process.

Male genitalia (Figs 1-3): Segment IX forms a complete ring with tergal part large and sternal part much narrower and constricted on the latero-ventral sides; segment X narrow and compact arranged in dorso-lateral position, dorsal side elevated, rectangular in dorsal view, caudal side with broad tooth directed ventrad; anal sclerites large, curved ventrad and with short root; apical band of segment X short, connected basally with the long tergal strap produced distally in short protruding process; coxopodite of inferior appendages angulated ventrally, with long and slender basal apodemes articulating with dorsal base of the phallotheca; ventral lobe of harpago elongate; phallic apparatus long, aedeagal complex with short dorsal process and broad, membranous ventral plate; ventral plate shortly excised apically, small and slender lateral lobes present; parameres long, crossing each other and bearing numerous bristles on the clubbed ends.



Figs 1-7: Male genitalia, *Rhyacophila baldensis* sp. n., **1** – lateral view, **2** – dorsal view, **3** – ventral view with ventral plate of aedeagus; *Rhyacophila banahawmontis* sp. n., **4** – lateral view, **5** – dorsal view, **6** – ventral view with ventral plate of aedeagus, **7** – ventral process of segment VII.

Remarks:

Rhyacophila baldensis sp. n. is a member of the *castanea*-group.

It stands close to the other Philippine species of the group by a similar structure of segment X. The form of the inferior appendages and the dorsal aspect of segment X provide the distinguishing features for separating the new species from its relatives.

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Rhyacophila banahawmontis sp. n.

(Figs 4-7, 22)

Holotype, ♂, Philippines, Luzon, Quezon, Mount Banahaw, Dolores, Kinabuhayan, 800 m, Cristal Falls, 14°02.11 N 121°27.02 E, 17. – 19.3.2000, W. Mey, K. Ebert & V. Richter (MFN).

Paratypes: 2 ♂♂, 3 ♀♀, same data as holotype (MFN).

Derivatio nominis:

The specific epithet is derived from the name of the terra typica, the lower elevations of Mount Banahaw in southern Luzon.

Length of forewing 5.5 – 6 mm, wing-span 11 – 12 mm; head and thorax dark brown; antenna brown, the basal third yellow-brown; ocelli white; forewings dark brown with numerous small white spots scattered over the whole forewing, especially dense in costal area; basal parts of veins with erected, black bristles; fork 4 in forewing as long or longer than its stalk; hindwings pale brown; abdominal segment VII with short sternal process.

Male genitalia (Figs 4-7): Segment IX complete ring with tergal part large and sternal part much narrower, constricted on the latero-ventral sides; segment X narrow and compact arranged in dorso-lateral position, dorsal side elevated, but flat and oval in dorsal view, caudal side without lateral teeth; anal sclerites moderately large, curved ventrad and with short root; apical band of segment X inconspicuous, connected basally with the long tergal strap which is produced distally in a short, freely protruding process; coxopodite of inferior appendages angulated ventrally and with long and slender basal apodemes articulating with dorsal base of phallotheca; ventral lobe of harpago elongate, rounded apically; phallic apparatus long, aedeagal complex with broad dorsal process and wide, membranous ventral plate; ventral plate shortly up-curved apically, lateral lobes absent; parameres long, crossing each other and bearing 6-8 bristles on the clubbed tips.

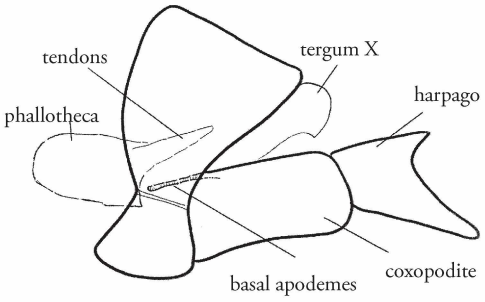

Fig. 8: Simplified sketch of male genitalia of *Rhyacophila.*

Remarks:

Rhyacophila banahawmontis sp. n. is a member of the *castanea*-group. It is obviously related to *R. negrosana* Mey, 1998. Both species lack the lateral lobes of the ventral plate of the aedeagal process.

Rhyacophila spinosellata - group

The group is established here to accommodate the following three new species and two previously known species. The latter species were assigned by Mey (1999) to a basal position within the *yosiiana*-group. The study of the new species revealed two synapomorphic characters (rectangular, plate-like dorsal process of phallotheca and large, un-rooted anal sclerites) which exclude the species from the *yosiiana*-group and necessitate the establishment of a group in its own. All included species are endemic to the Philippines.

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Diagnostic characters of the group:

- apodeme of coxopodite (= clasper tendon) not articulating with phallotheca (Fig. 9),
- pair of dorsal apodeme of phallotheca joining apical tergal strap (u-shaped piece),
- aedeagus tubular, without ventral or dorsal processes,
- median side of harpago sometimes with hooks or appendages,
- anal sclerites large, paired and without roots,
- rectangular, plate-like dorsal process of phallotheca,

***Rhyacophila amoyanensis* sp. nov.**

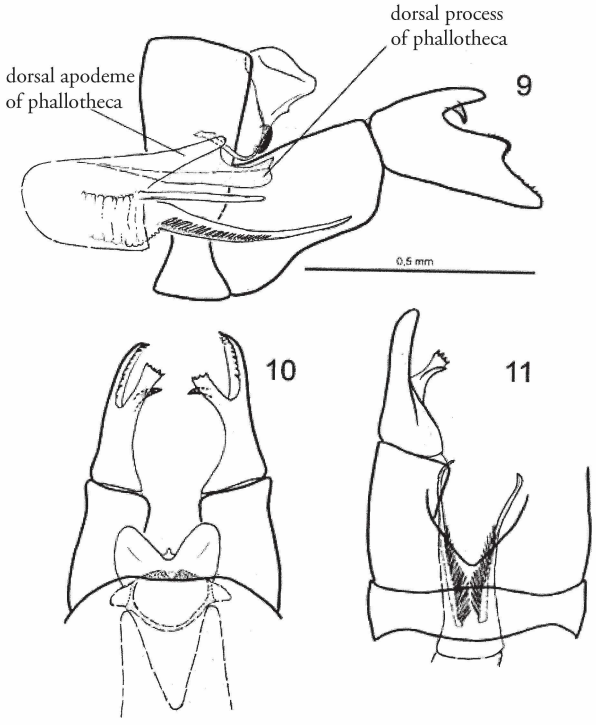
(Figs 10-12)

Holotype ♂, Philippines, Palawan, Litso, Amoyan Creek, 10 m, 57 km north of Puerto Princesa, 10.12.1965, leg. D. Davis (USNM).

Derivatio nominis:

The specific epithet is derived from the name of the small river, where the new species was collected.

Length of forewing 5.5 mm, wing-span 12 mm; head and thorax dark brown; frons and setal warts paler, vestiture black; ocelli white; forewings brown with darker pterostigma; legs light brown, spurs black; abdominal segment VII with short sternal process.



Figs 9-11: Male genitalia of *Rhyacophila amoyanensis* sp. n., **9** – lateral view, **10** – dorsal view, **11** – ventral view.

Male genitalia (Figs 10-12): Segment IX forms complete ring with tergal part large and sternal part much narrower, both indistinctly separated by short suture on the latero-ventral side; segment X arranged in dorso-lateral position, dorsal portion deeply excised forming two rounded lobes in dorsal view, lateral flanges with small tooth; anal sclerites moderately large, separated and without root; apical band of segment X fused basally and articulating with paired tendons of phallotheca; tergal strap absent; dorsal process of phallotheca produced distally in broad, freely protruding process; coxopodite of inferior appendages with slightly concave ventral margin and with slender basal apodemes probably articulating with lateral suture of segment IX by un-sclerotised membrane; ventral lobe of harpago elongate, with row of small teeth on dorsal margin, dorsal lobe short,

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truncate apically and with strong ventro-medially directed process; phallic apparatus short, aedeagus simple, slender tube without dorsal or ventral plates; parameres long, bearing row of black bristles along basal half.

Remarks:

R. amoyanensis sp. n. belongs to the *spinosellata* group. It differs from all other members of the group by the basally fused apical band of segment X (= u-shaped piece), the conspicuously shaped harpago and the long parameres.

Rhyacophila pilifera sp. n.

(Figs 13-17, 23)

Holotype ♂, Philippines, Luzon, Quezon, Mount. Banahaw, Dolores, Kinabuhayan, 800-900 m, Cristal Falls and Suplina Falls, 14°02.11 N 121°27.02 E 17. – 19.3.2000, W. Mey, K. Ebert & V. Richter (MFN).

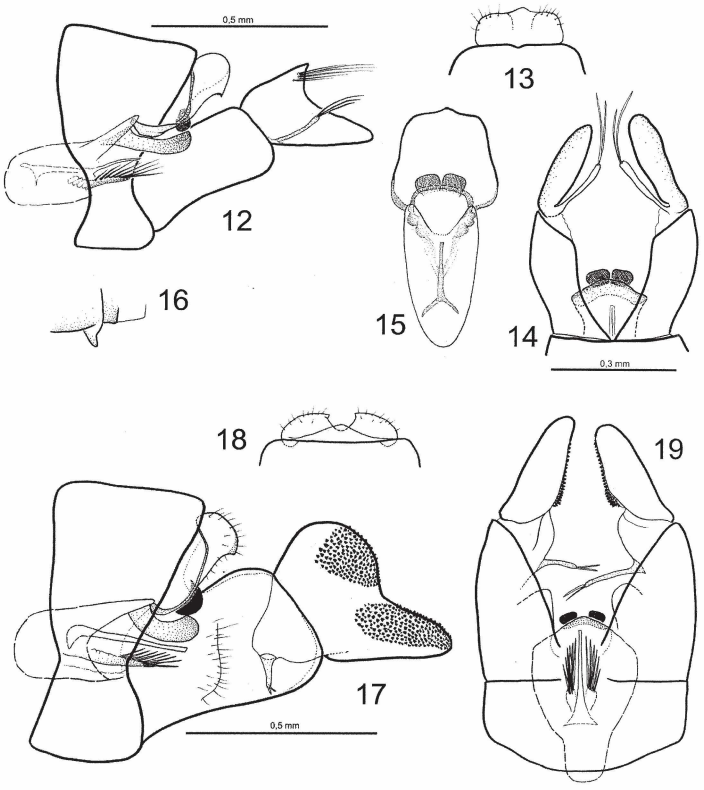
Paratypes: 3 ♂♂, same data as holotype (MFN).

Derivatio nominis:

The specific epithet is composed of the Latin words "pilus" (hair) and "fer" (carry) referring to the tuft of long hairs on the harpago.

Length of forewing 6 mm, wing-span 13 mm; head and thorax brown, frons and setal warts pale brown; vestiture on head black; ocelli white; antenna brown; forewings pale brown with darker pterostigma; fork 4 in forewing shorter than its stalk; in anal field of hindwing crossvein Cu2-A1 oblique; legs light brown, spurs black; abdominal segment VII with short sternal process.

Male genitalia (Figs 13-17): Segment IX forms complete ring with tergal part large and sternal part much narrower,



Figs 12-19: Male genitalia, *Rhyacophila pilifera* sp. n., **12** – lateral view, **13** – dorsal view, **14** – ventral view, **15** – phallotheca and segment X in dorsal view, **16** – ventral process of segment VII; *Rhyacophila cordilliera* sp. n., **17** – lateral view, **18** – dorsal view, **19** – ventral view.

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both indistinctly separated by a short suture on the latero-ventral side; segment X arranged in dorso-lateral position, dorsal portion compact with short medial process in dorsal view, lateral flanges with small tooth; anal sclerites moderately large, separated and without root; apical band of segment X separated basally and articulating only with paired tendons of the phallotheca; tergal strap absent; dorsal process of phallotheca produced distally in a broad, freely protruding process; coxopodite of inferior appendages with slightly concave ventral margin and with slender basal apodemes articulating with lateral suture of segment IX; ventral lobe of harpago elongate, with a filiform appendage originating from medial base and running in distal direction, its apex with 2-3 long bristles; dorsal lobe short, with a conspicuous tuft of long hairs on inner side; phallic apparatus short, aedeagus a simple, slender tube without dorsal or ventral plates; parameres short, bearing 8-10 black bristles.

Remarks:

Rhyacophila pilifera sp. n. belongs to the *spinosellata* - group. It differs from all other members of the group by the hair tuft of the harpago. It is related to the following species by the common presence of harpagal appendages.

Rhyacophila cordilliera sp. n.

(Figs 18-20, 24)

Holotype ♂, Philippines, Luzon, Ifugao, Mt. Polis, 2000 m, 13.11.1997, leg. W. Mey, K. Ebert & M. Nuss (MFN).

Paratypes: 3 ♂♂, Luzon, Benguet, Kabayan, Mount Tabayoc, 2300 m, 16°39 N 120°55 E, 22.-25.11.1997 (MFN).

Derivatio nominis:

The species is named after its range in the large mountain chain in northern Luzon which is known as Central Cordillera.

Length of forewing 7 – 7.5 mm, wing-span 15 – 16 mm; head and antennae dark brown; setal warts pale brown; thorax black on dorsal side; forewings brown with darker pterostigma; fork 4 in forewing shorter than its stalk; in anal field of hindwing crossvein Cu2-A1 oblique; legs light brown, spurs black; abdominal segment VII with short sternal process.

Male genitalia (Figs 18-20): Segment IX forms complete ring with tergal part large and sternal part much narrower, both indistinctly separated by short suture on the latero-ventral side; segment X arranged in dorso-lateral position, dorsal portion divided into a pair of bulbous parts, each with short, ventrally directed tooth; lateral flanges thin; anal sclerites large, separated and without root; apical band of segment X very short, separated basally and articulating only with paired tendons of phallotheca; tergal strap absent; dorsal process of phallotheca produced distally in broad, freely protruding process; coxopodite of inferior appendages with slightly concave ventral margin, a median flat lobe and with slender basal apodemes articulating with lateral suture of segment IX; lobes of harpago rounded, medial sides each with a patch of short, black spines; filiform appendage of harpago originating from medial base and running in medio-ventral direction, its apex with 2 short spines; phallic apparatus short, aedeagus a simple, slender tube without dorsal or ventral plates but with broader base; parameres short, bearing 6-8 black bristles.

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Remarks:

R. cordilliera sp. n. belongs to the *spinosellata* group. It differs from all other members of the group by the large and compact harpago in the male genitalia with two patches of strong, short spines on the inner side. It is related to the preceding species by the common presence of harpagal appendages on the ventral base.

3. 2. Phylogeny

The Philippines are a very diverse archipelago in terms of vegetation, climate, island sizes and topograpy. The great variety of available habitats is an ideal situation for arriving immigrants to survive and to settle permanently. The climatic cycles of the last 2 Mio years resulted in a repeated change of vegetation, shifting of vegetation zones and oscillations of island sizes. With each cycle species dispersed, extended and reduced their ranges or became isolated. These processes triggered speciation events and resulted in the formation of a wide spectrum of descendants ranging from simple species pairs to a multiplication of species. In Trichoptera the *hamifera* - group of the genus *Hydropsyche* Pictet is an example for the evolution of a large species swarm with more than 20 species distributed over the entire archipelago (Mey 2003). In contrast to *Hydropsyche*, species of *Rhyacophila* are ecologically more restricted, more localised and usually occur in smaller numbers. Although more species doubtlessly occur in the Philippines, but escaped collecting so far, the genus has not developed an adaptive radiation like *Hydropsyche*, with many species occurring in the same river system. Small headwater streams and spring areas remain the habitats of *Rhyacophila* species as on Borneo. Nevertheless, *Rhyacophila* exhibits a radiation, but of a different type. This radiation type is characterised by a pool of related species, each of them restricted or endemic to a single island. Congeneric species may occur sympatrically but in these cases they belong to different species groups. It is an open question, whether the species live only on the larger islands or also on smaller ones This would determine the size of the radiation. The Philippine species are distributed between two species groups. These are not closely related (Ross 1956, Schmid 1970)and are treated here separately:

The *castanea*-group contains four species which occur on three islands. The morphological analysis revealed that they are descendants of a single ancestor (Tab. 1, Fig. 25) that obviously immigrated from Borneo.

The *spinosellata*-group, established as new earlier in this paper, contains six species on five islands. In contrast to the *castanea* group it can be divided into three clades, which are morphologically well differentiated (Tab. 2, Fig. 26). Their ranges in the Philippines do not overlap. This supports the idea that the origin of these species is based on an old, perhaps Miocene colonisation and subsequent diversification. Alternatively, two or three independent colonisation processes could have caused the observed pattern. According to male genital characters the group is related to the *yosiiana*- and *betteni*-groups (Tab. 3, Fig. 27). The distribution of the former encompasses the Japanese Islands and the adjacent continental area (Fig. 31). The range of the latter group is confined to western North America.

3.3. Biogeography

Biogeographical research in the Philippines has to consider the biology and the ecological requirements of the studied taxa. On this basis two questions have to be answered: Where did the species come from or where did the group originate, and how did they manage to cross the sea?

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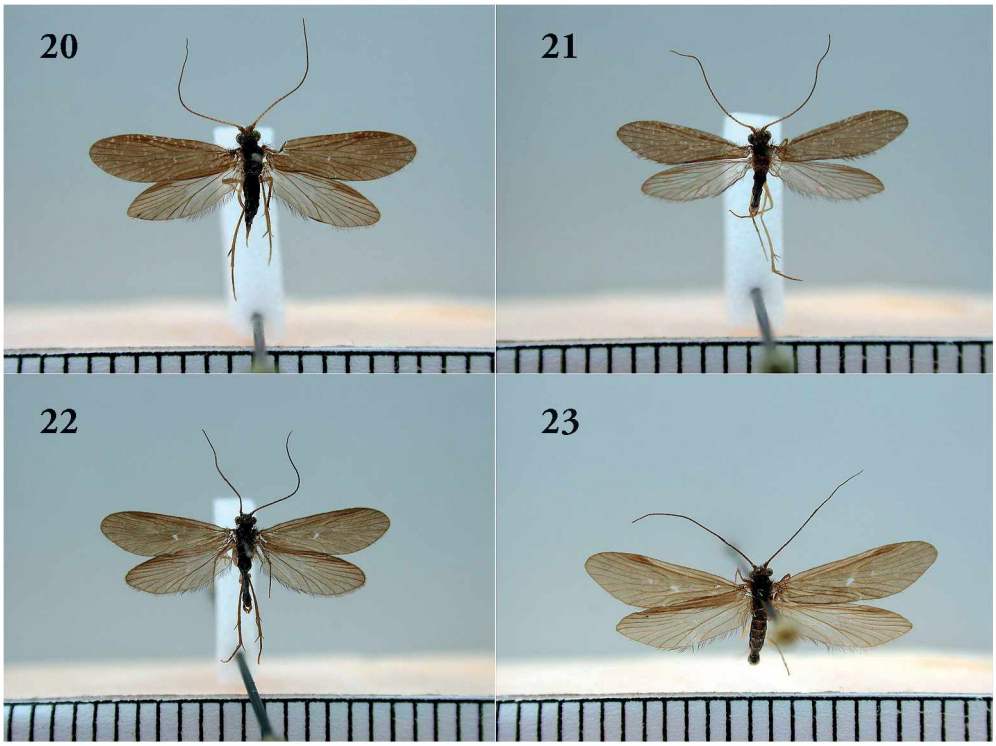
Rhyacophila is a large genus encompassing today more than 550 species. It has a predominantly Holarctic distribution. The Himalayan Region is home of a large number of species and species groups and can be considered their diversity centre (SCHMID 1989). From this region the numbers are declining towards South East Asia and Sundaland. Beyond Sulawesi, the genus is not known to occur (MEY 1999).

The aquatic larvae of nearly all known *Rhyacophila* species are free-living predators in running waters. They have a clear preference for temperate and cold streams. Accordingly, the majority of species dwell in the headwaters of rivers in mountain ranges from low to highest elevations. A few species, those of the Philippine included, have adapted to live in springs or spring areas. In the Philippines this habitat-type is not restricted to mountains but occurs in lowlands too. They are often associated with the drainage systems of lowland streams. *Rhyacophila* species have conquered this biotope and thus can occur outside mountain ranges. Within the Philippines localities of *Rhyacophila* are distributed from near sea level (10 m) to over 2000 m. In consequence, their potential distribution on the islands is much wider than the mountain zone and may encompass the entire area of an island. On Borneo the observed altitudinal gradient ranges from 200 m to over 3000 m above sea level (cf. HUISMAN & ARMITAGE 2011, MEY 2010). It may well be that suitable habitats in the lowlands are populated too, but those areas have largely been transformed into cultural land and human settlements, and suffered a loss of natural habitats such as springs or small streams. Historical or current records of occurring species are absent.

Adults are active during the day. They live in the lower vegetation of river banks as well as in the canopy layer. They are attracted to light, if a light source is in close vicinity to their habitats. According to



Figs 20-23: Adults of *Rhyacophila*, 20 – *R. baldensis* sp. n., female paratype, 21 – *R. banahawmontis* sp. n., male paratype, 22 – *R. pilifera* sp. n., male paratype, 23 – *R. cordilliera* sp. n., male paratype.

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personal observations the adults are weak flyers and only fly for short distances. The body is soft and not as well sclerotised as in temperate species. Thus, the imagines are prone of desiccation. When stored in glass vials they can survive half a day. The dispersal abilities of the adults appear to be poor. They cannot survive in open and sunny places and remain close to the waters where their larvae live. Within the forest, dispersal flights may happen along the streams and its ramifications, and at higher elevations between different water catchment areas. Mountain ridges do not represent serious barriers. The probability of successful migration between isolated forest patches separated by cultivated land, grassland or savanna is expected to be rather low. Adults of aquatic insects have different flight behaviours and dispersal abilities, but it is generally limited (Kovats et al. 1996). Active dispersal of flying *Rhyacophila* adults over sea straits to reach distant islands can be largely excluded.

It is still a matter of debate, whether the small continental terranes (e. g. the Zamboanga Peninsula, Mindoro Island) were permanently sub-aerial or not (Tan et al. 1988, de Jong & Treadaway 1993, Hall 1996). They are considered here as oceanic islands. All colonisation of the Philippine Islands except the Palawan and Busuanga Islands, which lies on the Sunda-Shelf, must have occurred by over water dispersal in a kind of passive transport. The often discussed rafts of tangled vegetation, carried to the sea by rivers in flood and drifting away to other islands, was a mechanism that could also have carried caddisflies. Floating islands of vegetation are often invoked as mechanism that permitted the dispersal of larger animals including mammals (Wallace 1880, Smith 2001).

During the Quarternary the climate was characterised by cycles of humid and dry periods. Humid periods with more extensive rainforest correlated with periods of high sea level and wider sea gaps. In dry periods, when sea gaps were at their narrowest, rainforests shrank to smaller patches and vegetation of the exposed Sunda shelf was dominated by savanna and grassland (Oosterzee 1997, Morley 2000). The then existing land bridges were of great significance for dispersal for savanna rather than for rainforest species. However, dense forest must have been present along streams and could have served as dispersal corridors. *Rhyacophila* species of lowland streams and springs could surely survive and disperse in this ecosystem. The expanded mega-islands, which appeared at times of low sea level, allowed dispersion to new areas and mountain ranges that later on became islands again. They also shortened the gaps between islands considerably and formed landbridge-like corridors along the modern Sulu Archipelago, bridging Borneo and Mindanao (Heaney 1985). But even at times of lowest sea level it remained a chain of neighbouring islands. The final crossing of narrow sea straits or sea surfaces probably happened by passive air transport. In the course of tropical thunderstorms and typhoons insects can be lifted to high altitudes, and are carried away by air currents. They are capable of transporting insect specimens over long distances. Each year in the summer months typhoons coming from the Caroline Basin of the West Pacific and running along the west coast of Mindanao and Luzon towards Taiwan or the Asian continent are recurrent events that affect, more or less strongly, the entire Philippine Islands. They have the potential to be important drivers of insect dispersal by passive transport and probably responsible for most of the colonisation processes that happen to occur in all groups of insects, including Trichoptera and *Rhyacophila* species.

Rhyacophila is represented in the Philippines by only two species groups, the *castanea* – and *spinosellata* groups, whereas four and five species groups including the *castanea*-group occur on Borneo and Sundaland respectively (Mey 1999, 2010). With nine species the *curvata*-group is the largest group in Borneo. Interestingly, the group has not been reported from the Philippines. Although there are some *curvata* – group species, dwelling in lowland streams in northern Borneo (e.g. *R. tawauensis* Mey, 2010) and therefore capable of dispersing in lowland areas, no species of the group has apparently arrived in the Philippines. It would not come as a surprise, were a member of the group to be eventually found in Mindanao.

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Tab. 1: Short description of relevant, male genital character states of the *R. castanea* group in the Philippines.

character		
number	apomorphic state	plesiomorphic state
1	lateral appendages of ventral lobe of aedeagus reduced in size, ribbon-like or absent	lateral appendages with slender stalk and broad apical half (dorsal view)
2	segment X compact in dorsal view, lateral flanges not prominent	segment X notched in dorsal and caudal view, lateral flanges prominent
3	lateral appendages of ventral lobe of aedeagus absent	lateral appendages of ventral lobe of aedeagus present, but thin

Tab. 2: Short description of relevant, male genital character states of the *R. spinosellata* group in the Philippines.

Character states		
number	apomorphic	plesiomorphic
1	Dorsal process of phallotheca broad and plate-like, fused basally with the phallothecal, dorsal apodemes	Dorsal process a slender extension of dorsal roof of phallotheca
2	Anal sclerites separate, without roots	Anal sclerites with roots
3	length of parameres shortened and with bundle of apical bristles	Paramers long, with bristles along median side, apex acute without bristles
4	Harpago with appendage on inner side bearing 2 apical spines	Harpago without appendage on inner side

Tab. 3: Short description of relevant, male genital character states of the *R. spinosellata*, *R. yosiiana* and *R. bettenei* groups.

Character states		
number	apomorphic	plesiomorphic
1	dorso-lateral apodemes of phallotheca connected to ventral side of segment X	dorso-lateral apodemes of phallotheca connected to apodemes of coxopodite
2	tergal strap absent	tergal strap present
3	Dorsal process of phallotheca broad and plate-like, fused basally with the phallothecal, dorsal apodemes	Dorsal process a slender extension of dorsal roof of phallotheca
4	Anal sclerites separate, without roots	Anal sclerites with roots
5	aedeagus with bifid tip	aedeagus tube-like, with simple tip
6	anal sclerites vestigial or absent	anal sclerites large, present

The *castanea* group has an extended range in South East Asia (Fig. 30) with many species but only one species, *R. argentipunctella* Kimmins, 1955, is known so far in Borneo. By contrast four species are described from the Philippines. They are closely related but live on different islands (Fig. 28). The ancestor of the Philippine species was a close relative of a group with *R. argentipunctella* as the only representative in Borneo. In the Pleistocene land-bridges developed and connected Borneo with Mindanao (Heaney 1985). Having arrived in Mindanao, probably along the Sulu Archipelago, the species was able to colonise southern Luzon and spread to northern Luzon. Even the Visayan Islands were reached with Negros as the hitherto only island with a species of this group (*R. negrosana* Mey, 1998). Occurrence on other Visayan Islands like Panay or Cebu is very probable (Fig. 28).

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The *spinosellata* group consists of six species. The first described species of the group were assigned to the *yosiiana* – group. Interestingly, the group has no close relatives on Borneo, Sundaland and in South East Asia (cf. Malicky 2010) (Fig. 31). *Rhyacophila brechlini* Mey, 1998, a Vietnamese species, was originally placed in the *yosiiana* group. Re-examination of the holotype revealed that it was misplaced in the group. In fact the species exhibit the primitive coupling of coxopodite and phallotheca by apodemes and the presence of a long tergal strap. The phallotheca is not firmly connected with the ventral side of segment X – the synapomorphy of the *spinosellata-*, *yosiiana-* and *betteni* groups. The species is probably better placed in the *scissa* group. The origin of the *spinosellata* group appears to be somewhat enigmatic. A closer examination of the genital morphology revealed that the oldest evolutionary line is represented by *R. amoyanensis* sp. n., discovered on Palawan (Fig. 29). From a geological viewpoint Palawan does not belong to the Philippines, but is situated on the Sunda Shelf close to Borneo (Hall 1996). At the height of the Pleistocene Palawan, including the Busuanga Islands further north, formed an elongate extension on the north-east margin of the fully exposed Sundaland shelf. Though in a peripheral position, it received the full spectrum of the Sundaland fauna (Oosterzee 1997, Heaney et al. 1998). *R. amoyanensis* sp. n. can be regarded as a Sundaland species. It is perhaps the surviving descendant of a more widespread species whose range extended through Borneo. Future fieldwork should clarify whether or not it is the only survivor. This ancestral Bornean species was able to spread over the exposed Sulu Archipelago and immigrated into Mindanao in accordance with the scenario described for the *castanea* group. Subsequent dispersion and speciation gave raise to different clades on the northern islands (Luzon, Mindoro) and on the southern islands (Negros, Mindanao) (Fig. 29).

Fig. 24: Cladogram of phylogenetic relationships within the *castanea* group in the Philippines (numbers refer to characters in table 1).

Fig. 25: Cladogram of phylogenetic relationships within the *spinosellata* group in the Philippines (numbers refer to characters in table 2).

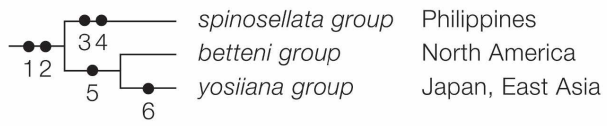

Fig. 26: Cladogram of presumed phylogenetic relationships of the *spinosellata* group (numbers refer to characters in table 3).

Alternative scenarios of immigration pathways into the Philippines were discussed by Mey (1999). They are based on a presumed, extended range of the *yosiiana* group towards southern China. From there, the route of a pre-Pleistocene ancestor into the Philippines should have run via Taiwan or was mediated by Mindoro, a continental terrane shifted with the opening South China Sea to its present position on the west side of the Philippines. Supporting arguments for these hypotheses might be provided by the discovery of hitherto undetected ancestral species still occurring in southern China and Taiwan. Up to now, such species have not been found. The discovery of three new species in the Philippines does not render these hypotheses less plausible. In fact, all proposed hypothesis try to explain an apparently extinction-mediated distribution pattern. Support for any scenario can be provided only if the extinction was not complete and surviving species still can be found. In any case, the range of the *spinosellata* group is that of a relict group separated by wide disjunctions from related groups. It is restricted to the Philippine Islands, and this makes the Philippines

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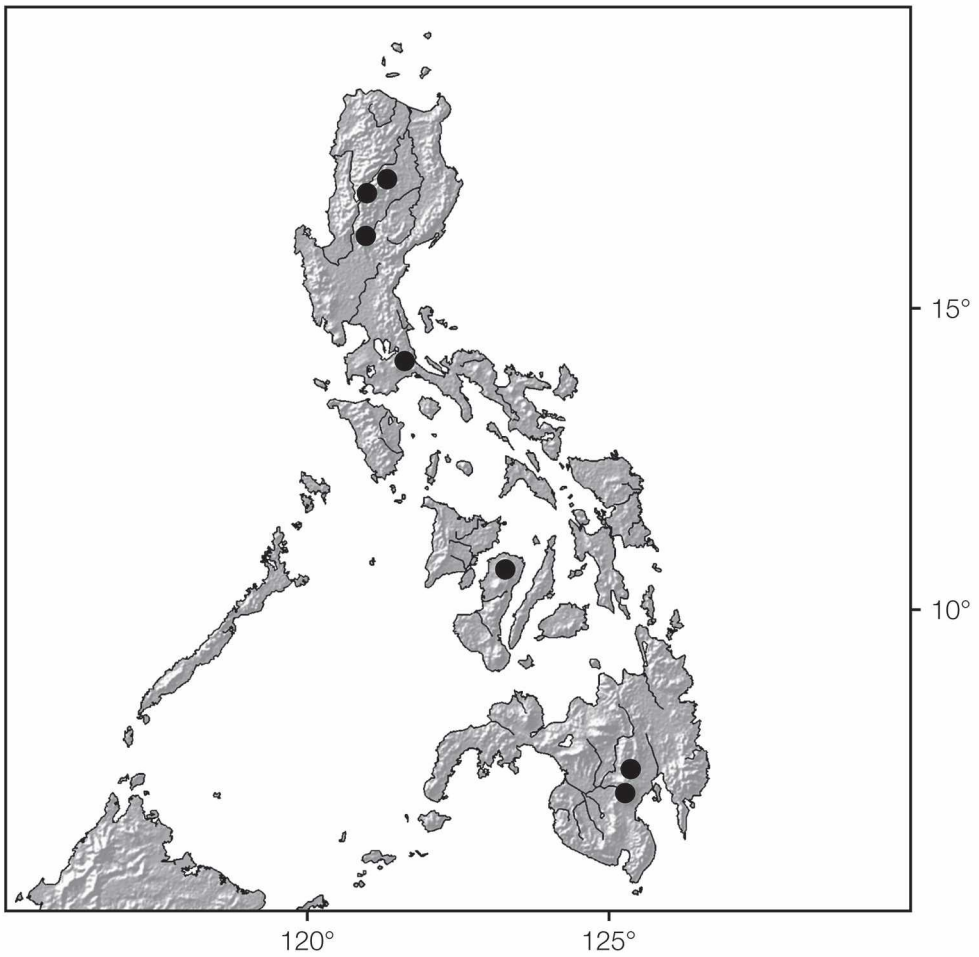

Fig. 27: Map of known localities of the *castanea* group in the Philippines.

an archipelago of refuge. There are probably additional groups in Trichoptera, and in other insect orders, for which the Philippines play the same role as a survival area. The search for additional relict groups is an exciting venture. The study of their phylogeny and biogeographic history might result in new arguments that can throw new light on the radiation of *Rhyacophila* and the herein presented attempt to find a plausible explanation.

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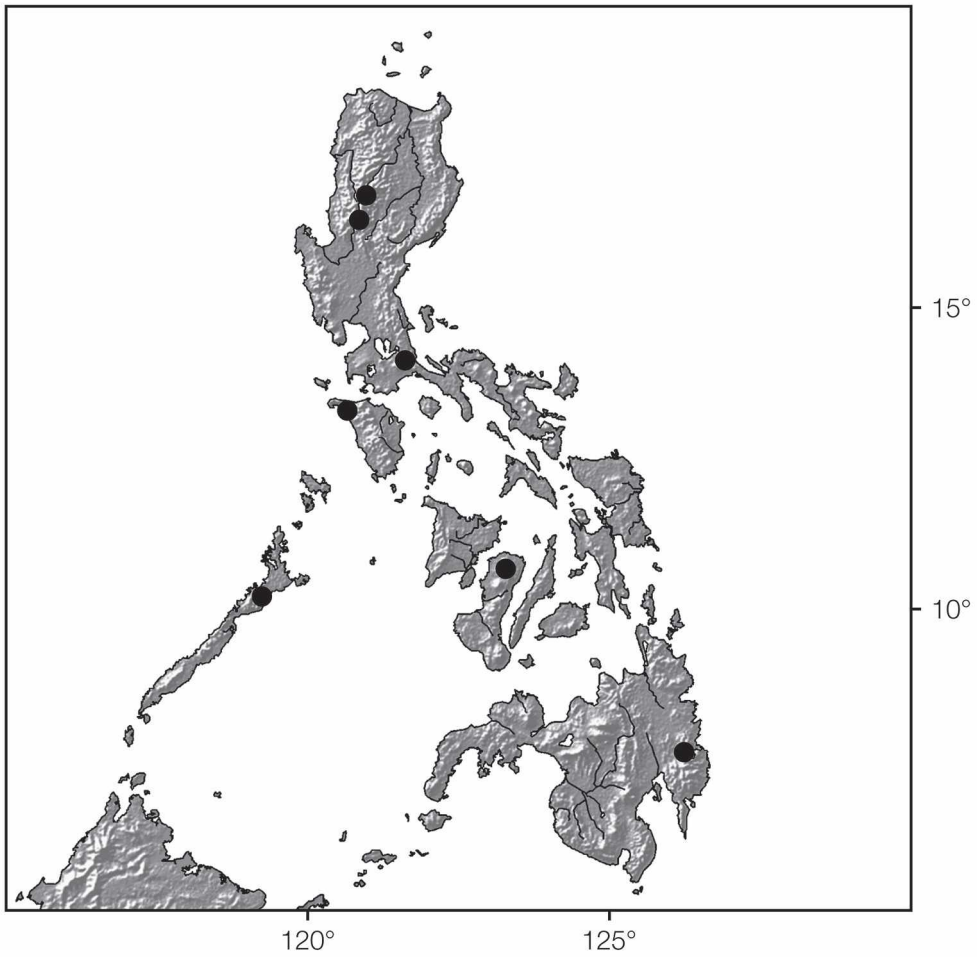

Fig. 28: Map of known localities of the *spinosellata* group in the Philippines.

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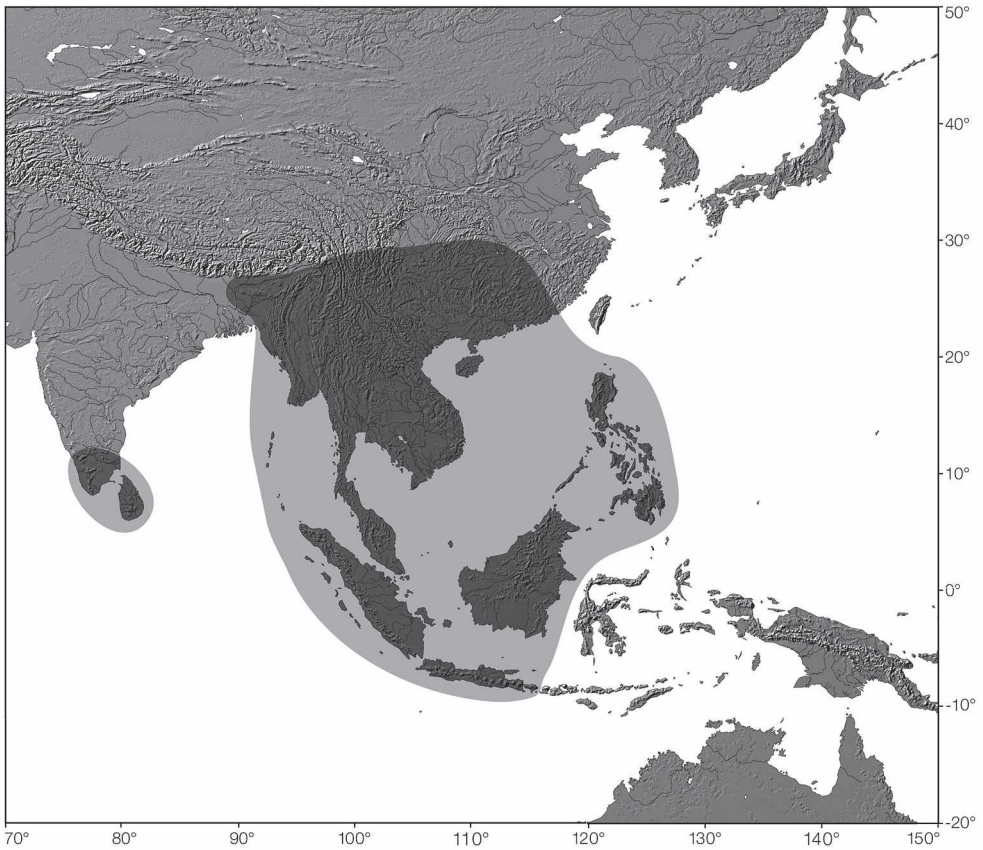

Fig. 29: Distribution map of the *castanea* group in Southeast Asia.

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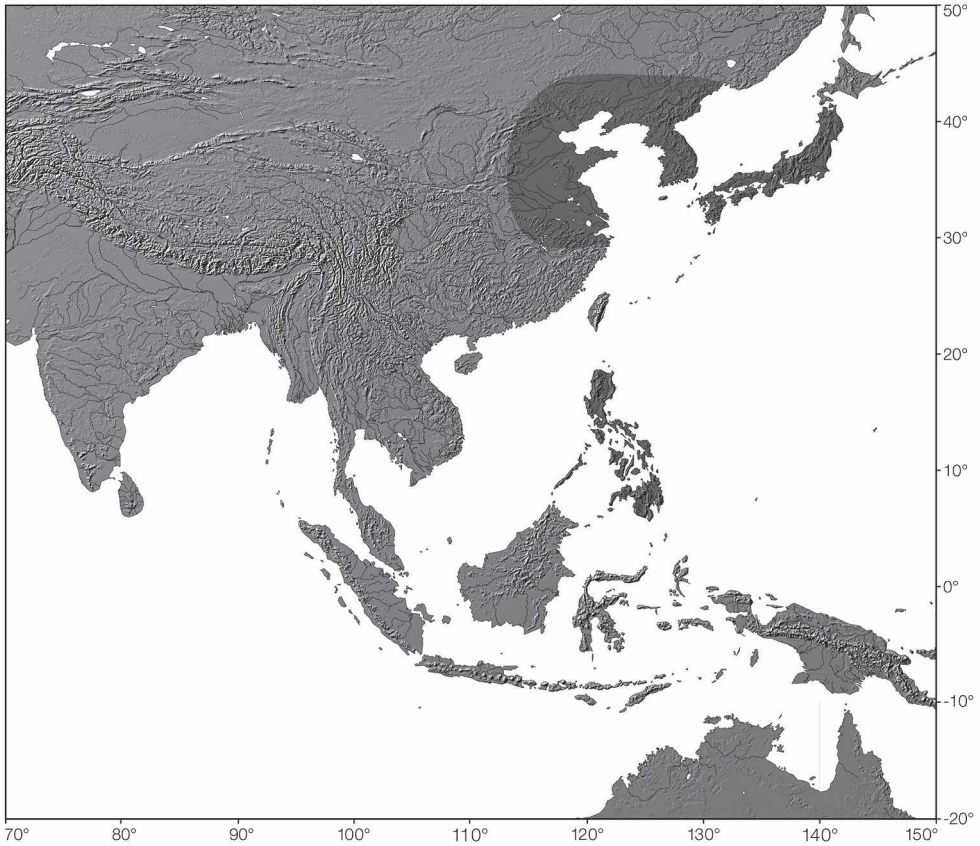

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